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What, if anything, can we learn from the fossil record about speciation in marine gastropods? Biological and geological considerations*

Warren D. Allmon[1,2] and Ursula E. Smith[2]

[1] Paleontological Research Institution, 1259 Trumansburg Road, Ithaca, New York 14850, U.S.A.

[2] Department of Earth and Atmospheric Sciences, Cornell University, Ithaca, New York 14853, U.S.A.

Correspondence, W. D. Allmon: wda1@cornell.edu

Abstract: Using fossils to study speciation requires careful analysis of the potential and limits of both biological and geological data. The most important biological data for a particular taxon includes to what degree species can be distinguished based only on hard-part morphology, what processes lead to speciation in that group today, and at what rates speciation occurs. Among the most important geological considerations is whether the incompleteness of the fossil record makes it possible to specify to within a reasonable degree of confidence when and where a putative speciation event took place. In benthic marine macroinvertebrates, the latter analysis is complicated by the "Common Cause" phenomenon: sea level change is both a major potential cause of gaps in the record and an important potential cause of evolutionary change. We consider the potential and limitations of fossil data for providing unique insight into the patterns and processes of speciation in marine shelled gastropods. A review of biological data shows considerable variation in mode of speciation and correlation between shell morphology and genetic divergence (cryptic species). Through examination of the fossil records of turritelline gastropods (Cerithioidea, Turritellidae) from Cenozoic deposits of the U.S. Gulf and Atlantic Coastal Plains and New Zealand, we propose simple tests for judging whether a particular fossil record is adequate for drawing conclusions about pattern and process of speciation. We conclude that the fossil record of marine gastropods *can* provide valuable information for studying species and speciation, but only if great care is used in evaluation of the data.

Key words: unconformities, completeness, cryptic species, Turritellidae

The role of the fossil record in investigating the origin of species is complex (Benton and Pearson 2001, Miller 2006). On one hand, species are at the center of paleontological studies of evolutionary tempo and mode (*e.g.*, Jackson and Cheetham 1999, Gould 2002), and have featured prominently in many paleontological studies of pattern and process in origination and extinction (*e.g.*, Jablonski 1986a, 1986b, Sepkoski 1998, Benton 2009). On the other, the fossil record is famously incomplete, and the degree to which fossil species are the same as those recognized in studies of modern organisms remains controversial, even among paleontologists (*e.g.*, Jablonski *et al.* 1986, Smith 1994, Levinton 2001, Pearson and Harcourt-Brown 2001, Coyne and Orr 2004).

Given this complexity, it is surprising that many paleontological studies have claimed to be addressing patterns and causes of "speciation" (albeit sometimes referred to more agnostically as "origination" or "diversification") without explicitly discussing whether they are really studying the same phenomena that neontologists call by the same name. Numerous paleontological studies, covering the entire Phanerozoic and virtually all preserved animal phyla, have hypothesized extrinsic or intrinsic causes for the origin of species (*e.g.*, Eldredge 1971, Hallam 1982, Ager 1983, Valentine and Jablonski 1983, Bayer and McGhee 1985, Cronin 1985, Gingerich 1985, Reif 1985, Vrba 1985, McRoberts and Aberhan 1997, Sandoval *et al.* 2001, McCune 2004, Alroy 2009). Presumably, these authors used the terms "species" and "speciation" assuming some connection to their use in studies of modern taxa. Yet there have been very few detailed examinations of exactly what "species" or "speciation" actually mean in such paleontological investigations (*e.g.*, Jackson and Cheetham 1999).

Gastropods are an especially important group in which to consider the role of the fossil record in elucidating evolutionary pattern and process at the species level. Their shells are commonly well-preserved and abundant in fossil assemblages, and they are among the most diverse clades of the past 100 million years (Erwin and Signor 1991, Morris and Taylor 2000). Fossil gastropods have been the subject of numerous influential studies of origination and extinction at the species

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level (*e.g.*, Gould 1969, Kauffman 1977, Hansen 1978, 1980, Williamson 1981, Jablonski 1986a, 1986b, 1987, 1997, Hansen *et al.* 1987, Erwin 1989, Roy 1994, Jablonski and Roy 2002, Glaubrecht 2011). The form of their shells, furthermore, has encouraged species-level paleontological studies of the relationship between form, development, and evolution (*e.g.*, Gould 1969, 1989, Geary 1988, Allmon 1994).

In this paper, we try to assess the feasibility of studying speciation in the fossil record by asking two questions: (1) what are the challenges in studying species and speciation in fossil marine gastropods, and how can they be overcome? (2) What can we learn about species and speciation in gastropods from such studies that we would not be able to learn (at all, or as easily) from studying modern forms? To address these two questions, we first undertake a review of the relevant *biological* issues—species and speciation in living marine gastropods (Krug 2011)—to see what generalizations might be applied (using uniformitarian reasoning) to fossils. We then undertake a mostly *geological* analysis of the options for confronting perhaps the most frequent obstacle in paleontological studies of speciation—incomplete preservation of stratigraphic and geographic ranges due to gaps in the fossil record—and we apply a set of simple tests for completeness to the fossil record of turritelline gastropods. We conclude with some tentative conclusions and a set of recommendations for how to study speciation in fossil marine gastropods in the future.

We devote most of our attention here to marine shelled gastropods (mostly vetigastropods and caenogastropods) because these are the most common gastropods in the fossil record. Our conclusions may or may not apply equally to the fossil records of other taxa, such as those on land or in freshwater (*e.g.*, Gould 1969, Reif 1985, Willmann 1985, Nützel and Bandel 1993, Glaubrecht 2011).

PREVIOUS STUDIES

What might be called "pre-modern" studies of species-level evolution in fossil marine gastropods (*e.g.*, Grabau 1904, Clark 1945, Fisher *et al.* 1964, Rodda and Fisher 1964) focused mainly on species description, stratigraphic distribution, and hypothesized anagenetic ancestor-descendant sequences based on stratophenetic phylogenies. Cladogenesis was not emphasized if it was mentioned at all.

More recent studies of speciation using the fossil record of marine gastropods can be placed in four categories. First are studies of single lineages or small subclades (*e.g.*, Hansen 1978, 1980, Schindel 1982, Allmon 1990, Geary 1990a, 1990b, 1995, Nehm and Geary 1994, McKinney and Allmon 1995, Gili and Martinell 2000, Kaim 2002). These studies frequently report correlations between environmental change and cladogenesis, but also document the occurrence of anagenesis as an apparent response to changes in environmental conditions. Although they may be satisfyingly specific, as noted by Wagner and Erwin (1995) such studies do not provide tests of the generality or relative frequency of any particular mode of speciation.

A second type of study surveys species across fossil assemblages, faunas, or clades, and attempts to correlate some kind of intrinsic or extrinsic factor with the appearance of new species (*e.g.*, Kohn 1990, Allmon 2001a, Jablonski and Roy 2002). A growing third group consists of similar studies that attempt to link molecular phylogenies, and the timing of cladogenetic events in these phylogenies as determined by molecular clocks, to major environmental perturbations, such as regional tectonism (*e.g.*, Williams and Duda 2008). Both fossil assemblage and molecular phylogenetic studies report positive correlations between environmental change and origination of new species. A fourth approach examines broader phylogenetic patterns, such as the distribution of plesiomorphies and the frequency of polytomies, as a source of insight into modes of speciation (*e.g.*, Wagner 1995, Wagner and Erwin 1995).

In sum, these previous studies of species and speciation in fossil gastropods are consistent with (but do not all require) speciation by allopatry. Most have suggested that cladogenesis is frequently the result of changes in the extrinsic environment, but also that some lineages respond to such changes by anagenetic transformation, in addition to or instead of cladogenesis. The relative frequencies of these various tempos and modes, however, remain unclear, as does the relative role of different environmental factors (sea level, temperature, etc.) in contributing to these different evolutionary patterns.

BIOLOGICAL ISSUES

Species recognition

The problem of taxonomic recognition and delimitation in shelled gastropods has long been recognized (*e.g.*, Gray 1835, Schander and Sundberg 2001, Wagner 2001). As has frequently been noted (but seldom documented), the vast majority of living shelled gastropod species descriptions have been (and continue to be) based exclusively on shell characters. This situation has led to the observation by paleontologists that fossil species (not just of gastropods) are effectively no different from most modern species (*e.g.*, Allmon 1990, Gould 2002: 785). When non-shell morphological characters, such as radula and soft-part anatomy, have been examined, however, such "conchological morphospecies" among caenogastropods are sometimes validated (*e.g.*, Michaux 1987, 1989, Kantor *et al.* 2008) and sometimes not (*e.g.*, Houbrick 1980, 1981). As molecular sequence data have become more

abundant, the topic of "species delimitation" has become more widely discussed, both in animals in general (Sites and Marshall 2003, 2004, de Queiroz 2007, Knowles and Carstens 2007, Shaffer and Thomson 2007, Wiens 2007, Hausdorf and Hennig 2010, Ross *et al.* 2010, Weisrock *et al.* 2010) and in marine gastropods in particular (*e.g.*, Reid *et al.* 2006, Bichain *et al.* 2007, Haase *et al.* 2007, Puillandre *et al.* 2009, Castelin *et al.* 2010).

Determining to what degree shell morphology reflects genetic divergence is further complicated by our lack of understanding of the causes for variation in shell characters in gastropods (*e.g.*, Olabarria and Thurston 2004, and references therein). Although a number of studies have demonstrated genetic components of morphological variation (*e.g.*, Janson 1982, Palmer 1984, Boulding and Hay 1993, Johannesson *et al.* 1993, Rolán *et al.* 2004), other studies have demonstrated significant ecophenotypic plasticity (*e.g.*, Wigham 1975, Hollander *et al.* 2005, 2006, Freiheit and Geary 2009, and references therein), and sometimes specifically used these conclusions to express varying degrees of caution about the recognition of fossil species (*e.g.*, Kemp and Bertness 1984, Palmer 1985, Palmer *et al.* 1990, Geiger and Groves 1999, Samadi *et al.* 2000).

As is true for other groups, species-level studies of fossil gastropods seldom explicitly state their operational concept of species. Exceptions (*e.g.*, Jung 1986, Allmon 1990, 1996, Nehm and Geary 1994, Freiheit and Geary 2009) usually compare morphometric variation in shell form of nominal modern species to fossils arrayed in time and space; consistently similar patterns are generally taken as sufficient evidence of practical equivalence.

The extreme case of discordance between such paleontologically recognizable morphospecies and genetically distinct evolutionary lineages is the occurrence of sibling or cryptic species. Although numerous examples were long ago identified in a variety of taxa (Mayr 1942, 1963), the recent proliferation of molecular data has led to a dramatic increase in the recognition of cryptic species across the animal kingdom, including in marine gastropods (*e.g.*, Knowlton 1993, 2000, Sáez and Lozano 2005, Bickford *et al.* 2007, Beheregaray and Caccone 2007, Pfenninger and Schwenk 2007, Castelin *et al.* 2010, Pérez-Ponce de Léon and Nadler 2010, Table 1).

Paleontologists usually acknowledge that they can say little about cryptic species (*e.g.*, Vrba 1980: 68, Gould 2002: 785ff, but see Gili and Martinell 2000, and Herbert and Portell 2004). Like most aspects of paleontology, however, the assumption is that knowledge of the occurrence of cryptic species among living forms can provide a reasonable assessment of the occurrence among extinct forms. There are two aspects to this problem. The first is common to all such applications of uniformitarianism: it is possible that the present is not an entirely reliable key to the past (*e.g.*, Kauffman 1987, Bottjer 1998, Allmon 2007). The second is that even if present and past are similar, we frequently know too little about the present. For example, Mayr (1963: 37) suggested that cryptic species "seem to be more common in some groups... than in others", yet this has proven to be controversial. Conflicting recent analyses of cryptic species across all phyla have argued either that the proportion of cryptic species is highly variable among higher taxa (*e.g.*, Bickford *et al.* 2007, Trontelj and Fišer 2009, Poulin 2010), or that it is approximately equal (Pfenninger and Schwenk 2007). If the former, then it might in principle be possible to assess the relative frequency in different taxa, and then apply the results to their respective fossil representatives. If the latter holds, then (at least for comparisons among taxa) cryptic species could be ignored (although we still might not know what the actual absolute frequency is in a particular taxon).

The occurrence of cryptic species in marine gastropods has not previously been the subject of careful analysis, and the list of published reports in Table 1 provides only sparse insight into what the actual pattern might be. It is possible that the taxonomic distribution of cryptic species in Table 1 is representative of the actual distribution among gastropod higher taxa. It is more likely, however, that the abundance of published reports of cryptic species in, for example, *Littorina* and related forms reflects the relatively intense level of study that these taxa have received from ecologists and systematists, as much or more than the actual frequency of cryptic species within the group. Similarly, the seemingly high number of reports among cones and turrids may be related simply to their very high species diversity.

In summary, data currently available support the conclusion that cryptic species do occur widely among living shelled marine gastropods, and that this should be taken into account when thinking about fossils (*e.g.*, speciation rates based on fossils are minimum estimates). At least some instances of otherwise cryptic species can be recognized in fossils based on differences in the larval shell (Gili and Martinell 2000, Herbert and Portell 2004), and this might be a fruitful area for future work. It remains to be determined, however, whether cryptic species are more common in marine gastropods than in other higher taxa, whether all marine gastropod groups show equal proportions of cryptic species, or what the pattern of occurrence of cryptic species was in marine gastropods in the geological past.

Modes of speciation

New species can arise in a variety of ways (Table 2). Most recent studies of speciation in marine gastropods have concluded that speciation is predominantly allopatric (*e.g.*, McManus 1985, Knight *et al.* 1987, Vermeij 1987, Denis *et al.* 1993, Collins *et al.* 1996, Hellberg 1998, Marko 1998, Pudovskis *et al.* 2001, Collin 2003, Meyer 2003, Williams and

Table 1. Published studies documenting cryptic species in shelled marine gastropods. Genera are listed as in the references cited.

Family	Genus	References
Patellidae	*Patella* Linnaeus, 1758	Evans (1953), Ridgway *et al.* (1998)
Lottiidae	*Lottia* Gray, 1833	Crummett and Eernisse (2007)
	Collisella Dall, 1871	Murphy (1978)
	Notoacmaea Iredale, 1915	Simison and Lindberg (1999), Nakano and Spencer (2007)
Lepeteodrilidae	*Lepetodrillus* McLean, 1988	Johnson *et al.* (2008), Vrijenhoek (2009)
Trochidae	*Oxystele* Philippi, 1847	Heller and Dempster (1991)
	Diloma Philippi, 1845	Spencer *et al.* (2009)
	Austrocochlea Fischer, 1885	Parsons (1996)
Turbinidae	*Astralium* Link, 1807	Meyer *et al.* (2005)
	Alviniconcha Okutani and Ohta, 1988	Denis *et al.* (1993)
Provaniidae		
Calyptraeidae	*Calyptraea* Lamarck, 1799	Gallardo (1977, 1979)
	Bostrycapulus Olsson and Harbison, 1953	Collin (2005)
	Crepidula Lamarck, 1799	Gallardo (1977, 1979), Hoagland (1977, 1984, 1986), Collin (2000, 2001), Chaparro *et al.* (2002), Véliz *et al.* (2003), Schmidt *et al.* (2006)
Littorinidae	*Littorina* Ferussac, 1822	Heller (1975), Sacchi *et al.* (1977), Murray (1979), Wilkins and O'Regan (1980), Bandel and Kadolsky (1982), Mastro *et al.* (1982), Moyse *et al.* (1982), Raffaelli (1982), Sacchi (1984), Ward and Janson (1985), Reid (1986), Janson (1987), Chow (1987), Ward (1990), Warwick *et al.* (1990), Boulding *et al.* (1993), Crossland *et al.* (1993), Rolán-Alvarez *et al.* (1995a, 1995b), Grahame *et al.* (1997), Clarke *et al.* (1999), Tatarenkov and Johannesson (1998), Wilding *et al.* (2000), Hohenlohe (2002)
	Nodilittorina Martens, 1897	
	Bembicium Philippi, 1846	Reid (1988)
	Risellopsis Kesteven, 1902	
Rissoidae	*Alvania* Risso, 1826	Oliverio (1996)
	Rissoa Freminville, 1814	Rehfeldt (1968), Munksgaard (1990), Oliverio (1996)
	Frigidoalvania Warén, 1974	Quattro *et al.* (2001)
Vermetidae	*Dendropoma* Mörch, 1861	Safriel and Hadfield (1988), Calvo *et al.* (2009)
	Petaloconchus Lea, 1843	Weinberger *et al.* (2010)
Buccinidae	*Nassaria* Rafinesque, 1815	Castelin *et al.* (2010)
	Sassia Bellardi, 1873	Castelin *et al.* (2010)
Nassariidae	*Nassarius* Dumeril, 1806	Oliverio and Tringali (1992), Oliverio (1996), Sanjuan *et al.* (1997)
Muricidae	*Chicoreus* Montfort, 1810	Castelin *et al.* (2010)
	Nucella Röding, 1798	Palmer *et al.* (1990), Marko (1998)
	Leptoconchus Rueooell, 1834	Gittenberger and Gittenberger (2006)
Volutidae	*Alicithoe* H. and A. Adams, 1853	Castelin *et al.* (2010)
Olividae	*Amalda* H. and A. Adams, 1853	Michaux (1987)
Conidae	*Conus* Linnaeus, 1758	Chaney (1987), Vallejo (2005), Duda *et al.* (2008, 2009)
Turridae	*Mangelia* Risso, 1826	Oliverio (1996)
	Bela Leach, 1847	Oliverio (1996)
	Raphitoma Bellardi, 1848	Oliverio (1996)
	Haedropleura Monterosato, 1883	Oliverio (1996)
	Gemmuloborsonia Shuto, 1989	Puillandre *et al.* (2010)
	Xenuroturris Iredale, 1929	Kantor *et al.* (2008)
Bullidae	*Bulla* Linnaeus, 1758	Malaquias and Reid (2008)

Reid 2004, Donald *et al.* 2005, Meyer *et al.* 2005, Paulay and Meyer 2006, Reid *et al.* 2006, Malaquias and Reid 2009, Castelin *et al.* 2010). Numerous recent authors have also suggested, however, that non-allopatric modes of speciation (especially ecological speciation) are important in marine gastropods (*e.g.*, Hellberg 1998, Pickles and Grahame 1999, Cruz *et al.* 2004, Hollander *et al.* 2005, Vallejo 2005, Conde-Padín *et al.* 2007, Glaubrecht 2009, Johannesson 2009, Krug

Table 2. Modes of speciation (modified from, *inter alia*, Lynch 1989, Wagner and Erwin 1995, de Queiroz 1998, Coyne and Orr 2004).

	Mode	Geography	"Allopatric mechanism"	Parent:daughter population size
I.	Anagenesis			
II.	Cladogenesis			
A.		Allopatric		
1.			Vicariance	
				Parent ≅ daughter (bifurcation, dumbbell allopatry)
				Parent >> daughter (peripatry)
2.			Dispersal	Parent >> daughter (peripatry)
B.		Sympatric		

2011). It remains to be determined what the actual relative frequency is between allopatric and non-allopatric speciation, or whether it varies among clades.

Within the allopatric mode and its two principal geographic mechanisms, vicariance and dispersal, considerable attention has been devoted to the influence of larval biology on probability or rate of speciation in marine gastropods (*e.g.*, Hansen 1978, 1980, Scheltema 1978, Jablonski 1986a, Jablonski and Lutz 1980, 1983). The most widely held view is that species with larvae that spend more time in the plankton (mostly planktotrophs, but including some non-planktotrophs) have higher dispersal probabilities, wider geographic ranges, and lower rates of isolate formation, genetic divergence, and speciation. Species with larvae that spend less or no time in the plankton, on the other hand, are generally thought to have lower dispersal probability, narrower ranges, and higher rates of isolation, divergence, and speciation (*e.g.*, Valentine and Jablonski 1983, Jablonski 1986a). Planktotrophy is widely viewed to be the primitive condition in most clades of caenogastropods (Jablonski and Lutz 1983). Thus, the evolution of non-planktotrophy in a lineage or clade is often seen as an event that may lead to an increase in speciation (*e.g.*, Hansen 1978, 1980, Cunha *et al.* 2005). For the great majority of caenogastropod clades, however, the proportion of species with planktotrophic versus nonplanktotrophic larvae through time is not known in any detail.

The frequently wide geographic distribution of marine invertebrate species has been called a paradox by some authors, who have wondered how isolation can occur in the presence of so much dispersal and (presumably) gene flow (Palumbi 1992, 1994, Neigel 1997, Williams and Reid 2004, Meyer *et al.* 2005). Several solutions to this paradox have been proposed:

(1) Allopatric speciation in many marine environments (especially shallow coastal areas) may frequently occur at smaller geographic scales than previously recognized (Meyer *et al.* 2005).

(2) High dispersal potential does not necessarily imply a paucity of geographic barriers (*e.g.*, Waters *et al.* 2005), nor does low dispersal potential of larvae necessarily imply low dispersal of adults (Donald *et al.* 2005, Imron *et al.* 2007). At least some widespread species may also be more likely to form more isolates (and therefore give rise to more descendant species) simply because they are larger and inhabit wider geographic areas, and perhaps also a wider array of environments (Scheltema 1978).

(3) Diversification in at least some clades may be greatest at intermediate levels of dispersal (Paulay and Meyer 2002, 2006), except at very local scales, where species complexes (clusters of very closely related species) appear to be most frequent among low-dispersal species (Paulay and Meyer 2006, Castelin *et al.* 2010).

(4) Narrow geographic ranges in daughter species might make them more extinction-prone, but might also permit greater "species packing", enhancing survival and allowing for higher local species diversity (*e.g.*, Jablonski and Roy 2002, Meyer *et al.* 2005).

(5) As mentioned above, we may have underappreciated the occurrence of non-allopatric modes of speciation (*e.g.*, Johannesson 2009, Krug 2011).

Other variations of conventional allopatric speciation have been reported in modern marine gastropods. Coincident geographic ranges of apparently ecologically similar species, for example, do not always produce coincident responses to extrinsic environmental disturbance "suggesting that relatively minor differences in traits such as pelagic larval duration or microhabitat association may profoundly impact phylogeographical structure" (Crandall *et al.* 2008: 611). Sister taxa are not always divided by broad and long-lasting geographic barriers; "transient allopatry" or purely ecological barriers may suffice (Hellberg 1998). It has also been suggested that mode of speciation may differ under different geographic conditions; coastal species, for example, may be more likely to show speciation by peripatric dispersal and may favor the sympatry of sister taxa, whereas broad regions with many oceanic islands (such as the modern Indo-West Pacific) may be sites of more vicariant allopatry and less sister species overlap (Valentine and Jablonski 1983, Hellberg 1998).

Thus, living marine gastropods appear to show a variety of modes of speciation. There is clearly ample evidence for speciation by allopatry (via both vicariance and dispersal), but the linkage between larval dispersal and probability of speciation is neither simple nor uniform across taxa. There is, furthermore, strong (and perhaps growing) evidence for the occurrence of sympatric, or ecological, modes of speciation, apparently driven largely by relatively small shifts in habitat preference within otherwise continuous populations. It unfortunately remains unclear, however, whether there are broad intrinsic or extrinsic factors that might bias species formation toward one mode more than another.

Rates of speciation

Discussions about "rates of speciation" focus on two different phenomena, which are not necessarily closely related. The first is the time interval between speciation events within a lineage ("species per million years" or the "speciation interval") (Raup 1978, Coyne and Orr 2004). The second is the time it takes for a daughter population to diverge sufficiently from the parent population to achieve reproductive isolation (the "transition time", "time for speciation", "waiting time to speciation", or "duration of speciation") (Gavrilets 2000, Coyne and Orr 2004, McCune 2004, Curnoe *et al.* 2006). Speciation intervals are generally longer than transition times (and can be *much* longer) because lineages do not begin to branch immediately after they arise. Speciation intervals are estimated in a variety of ways, usually based on the fossil record. Transition times are generally more difficult to estimate, because this requires knowledge of when speciation begins, and so most estimates of "speciation rates" in the literature are actually "speciation intervals".

In rare instances such as lakes that preserve extremely high-resolution fossil records, transition times can be estimated with high precision (*e.g.*, McCune 2004). Estimates of "divergence times" between geminate species that are commonly used to calibrate molecular clocks (*e.g.*, Marko 2002)—equivalent to estimates of "speciation duration" in phylogeography (Avise 2000)—are not necessarily equal to transition times; differences between geminates could have been generated more quickly than divergence times based on the fossil record, and so such estimates represent maximum values. Other direct estimates of transition times have been made from the fossil record (summarized by Gould 2002: 852), ranging from 5,000 years for the Quaternary origin of dwarfed woolly mammoths on Wrangel Island, Alaska, to 73,000-275,000 years for the marginellid gastropod genus *Prunum*, to 100,000-200,000 years in a genus of Cretaceous marine ostracodes.

Transition times in the fossil record have also been discussed in the context of the theory of punctuated equilibrium (Eldredge and Gould 1972). Eldredge (1985: 189), for example, informally estimated that speciation usually takes "five to fifty thousand years". In attempting to define when a speciation event is "punctuated", as opposed to gradual, Gould repeatedly argued for a relative metric, such as 1-2 percent of the total subsequent duration of the species produced (Gould 1982, 2002: 768). Such a definition, he said, would allow "up to 100,000 years for the origin of a species with a subsequent life span of 10 million years" (the estimate for the average species of marine bivalves, Stanley 1979). Gould added, however, that he believed "that most events of speciation occur much more rapidly" (Gould 1982: 84).

Compilations of speciation intervals (Stanley 1979, Coyne and Orr 2004: 419) show that, although values range from very short (4,000 years for cichlid fishes in Lake Nabugabo, Uganda) to very long (several hundred million years for Notostracan crustaceans), most cluster between 1 and 20 million years. The compilation of Coyne and Orr (2004) yields a mean speciation interval for all taxa (protists to mammals) of 6.5 million years, with marine invertebrates showing higher values (most groups between 6 and 16 million years) than terrestrial plants, which in turn show longer intervals than terrestrial and freshwater insects and vertebrates. Marine gastropods show a mean value of 14.9 million years (Stanley 1979). Several more recent studies of divergence times of geminate pairs of marine gastropods across the Central American Isthmus indicate somewhat lower values (5-10 million years, which, as mentioned above, represent maximum values) (Collins 1996, Marko 2002).

Based on all of these data, the average lineage of marine gastropod appears to produce a new species roughly every 5-15 million years. Each of these new species, however, may actually arise in less than 100,000 years.

GEOLOGICAL ISSUES

The fossil record is incomplete (*e.g.*, Darwin 1859, Allmon 1989, 2001b, Valentine 1989, McKinney 1991, Foote 2001, Holland 2000, Kidwell and Holland 2002, Peters 2006, Smith 2007) because of a set of biological, geological, and taphonomic factors (referred to as "extrinsic biases" by Peters 2006). Our knowledge of the part of the record that *is* preserved is also incomplete (Signor and Lipps 1982, Marshall 2010) because of a set of sampling and taxonomic factors ("intrinsic biases", Peters 2006). Extracting biological signals from the fossil record therefore requires us to evaluate to what degree observed patterns in the fossil record are the result of biological changes, and to what degree the result of the structure of the stratigraphic record (*e.g.*, Kidwell and Flessa 1995, Holland 2000, Kidwell and Holland 2002, Peters 2006, Smith 2007).

The basic data for studying speciation in the fossil record consist of the distribution of appearances ("originations") of new taxa (usually referred to as "first appearance datums", or FADs, Van Couvering and Berggren 1977, Schoch 1989, Allmon 2003) in time and space. Because of the incompleteness of the record, however, an FAD for a taxon is in almost all cases later than—and in a different location from—the actual evolutionary first appearance ("EFA"). The greatest differences between FAD and EFA are likely to occur in association with unconformities—surfaces (representing intervals of time) of non-deposition and/or erosion. This has been called the "Unconformity Bias" of the fossil record (Holland 2000, Peters 2006). If FADs are coincident with an unconformity, then the time and/or place of the EFA may be highly uncertain because of the missing record (Jablonski 1980, Haq and Worsley 1982, Schoch 1989, Holland 2000). Indeed, the occurrence of multiple coincident FADs (and/or last appearances, or LADs) has been taken under some circumstances to be indicative of otherwise unrecognizable unconformities (Shaw 1964, Schoch 1989: 204). In such circumstances, a frequent assumption of paleontologists, "barring any evidence to the contrary, is generally that a FAD represents the immigration of a species shortly after its origination (evolution) in some unspecified area" (Schoch 1989: 201), but how "shortly after" and where that "unspecified area" was are usually left unstated. Thus, an FAD may be caused by a variety of frequently unknown phenomena, including *in situ* speciation or immigration, occurring at some unknown time (Fig. 1).

In the case of marine taxa, there is another important consideration. Major unconformities in marine stratigraphic sections are frequently the result of changes in sea level, which leads to non-deposition and/or erosion. Yet sea-level change is also one of the major environmental influences on benthic marine organisms on geological time scales, affecting habitat size and environmental conditions. In the context of the allopatric model of speciation, sea level change might theoretically cause cladogenesis by isolating populations of a species along a shallow shelf (Fig. 2, Valentine and Jablonski 1983, McKinney and Allmon 1995, Allmon *et al.* 1998). Sea level change is thus a major potential cause of both unconformities and evolutionary change (*e.g.*, Loutit *et al.* 1988, Patzkowsky and Holland 1993, Holland 1995, 2000, 2003, Allmon 2004, Allmon and Harries 2008). This has been called the "Common Cause" hypothesis (Peters and Foote 2002, Peters 2006).

In an analysis of all fossil genera of marine animals through the Phanerozoic, Peters (2006) found no significant correlation between mean duration of temporal hiatus at unconformities and genus origination rate (represented by FADs) in the following interval. Peters suggested that this result provides at least circumstantial support for the Common Cause hypothesis (such a conclusion would, of course, require close correlation between patterns of origination of genera and species, which might not be the case). The Common Cause phenomenon is likely a major issue in paleontological studies of speciation, since numerous studies, in a variety of taxa, have proposed connections between sea level change and species origination (*e.g.*, Hallam 1984, Bayer and McGhee 1985, Potts 1985, Rawson 1993, McKinney and Allmon 1995, McRoberts and Aberhan 1997, O'Dogherty *et al.* 2000, Sandoval *et al.* 2001, Zhang *et al.* 2006). Most of these studies, however, have not explicitly considered the potential effects of the Unconformity Bias.

Tools for dealing with the problem

The significance of a mismatch between a species' FAD and EFA thus depends on the "completeness" of its fossil record. A number of authors have attempted estimates of the overall completeness of the paleontological record (*e.g.*, Allmon 1989, Valentine 1989, McKinney 1991, Foote 1996,

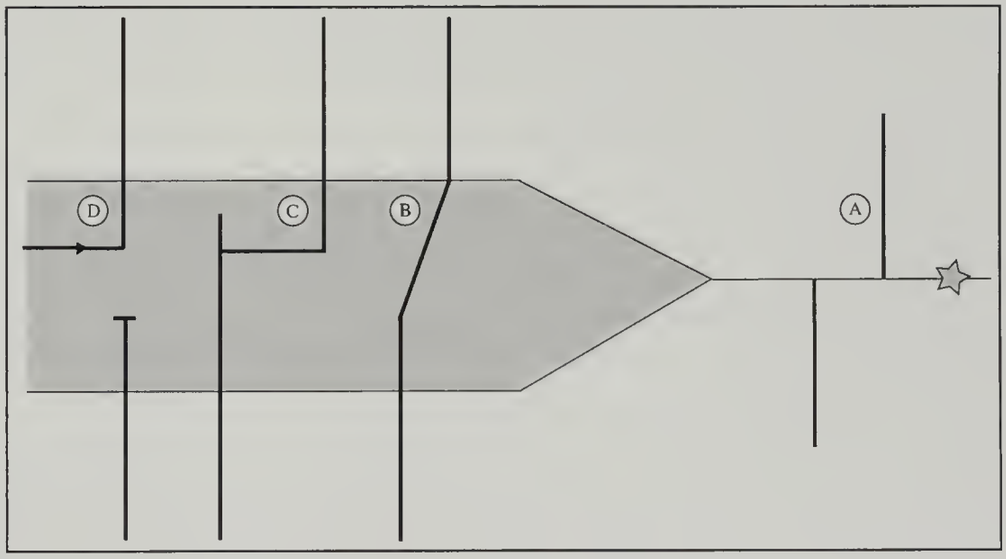

Figure 1. Schematic diagram showing three possible evolutionary events that may take place during a temporal hiatus (shading), coinciding with an unconformity (marked by the star). A, Observed pattern of an FAD immediately above the unconformity, coincident with the LAD of a potential ancestor immediately below the unconformity. This pattern could be caused by: B, anagenetic transformation of the older lineage into the younger lineage; C, cladogenetic event, producing the younger lineage as a daughter species of the older lineage, followed by extinction of the parent lineage; or D, extinction of the earlier lineage and invasion of the new lineage from outside the region.

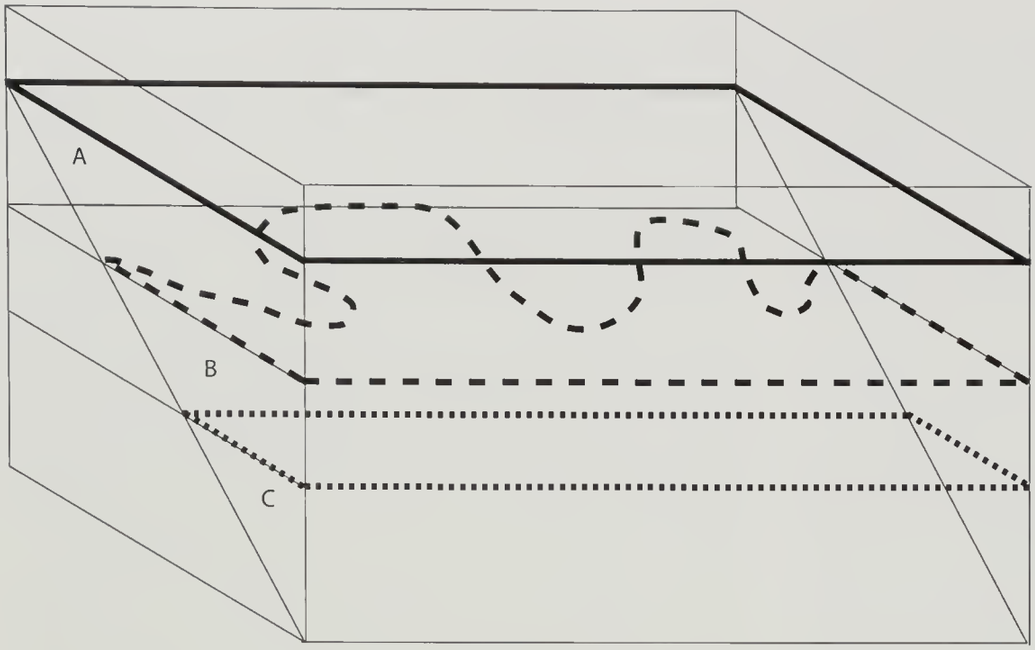

Figure 2. How change in sea level can cause allopatric speciation. As sea level falls from level A to level B, or rises from level C to level B, topographic irregularities on the shelf lead to formation of separate embayments or basins, which could isolate populations of a species.

1997, 2001, Foote and Sepkoski 1999, Benton *et al.* 2000). These techniques, however, are at too coarse a scale for the purposes described here. Others have developed techniques for estimating confidence limits for the stratigraphic range of a particular taxon (Marshall 2010 and references therein). These approaches are also not applicable to our situation because they cannot estimate missing ranges beyond the first and last recorded appearance of a taxon (Smith 2007).

We have therefore here developed four tests (Fig. 3) that can be applied to estimating *the confidence with which we can conclude that an observed FAD of a particular fossil species is roughly coincident with the actual time and place of the speciation event (EFA) that gave rise to that species.* The first of these tests takes a geographic perspective, attempting to estimate the likelihood that immigration explained an FAD. All other factors being equal, if no source of phylogenetically appropriate immigrants can be identified at roughly the same or slightly earlier time interval as an FAD, this will increase our confidence in equating the FAD with the time and place of the EFA. The other three take a temporal perspective, attempting to estimate how much time elapsed between a species' FAD and its EFA. All other factors being equal, the shorter the time, the greater our confidence could be in equating FAD and EFA.

Test #1: Potential sources of immigration

An FAD could record only *local* first appearance, *i.e.*, the species could have originated elsewhere and the FAD marks only the immigration event into the area represented by outcrops or collections (*e.g.*, Schankler 1981, Schoch 1989) (Fig. 3). The probability of such immigration can, in principle, be assessed if potential sources of immigration can be identified and analyzed for possible ancestors or sister species of the taxon showing the first appearance. This approach starts with specifying the "total potential source area" for a species, consisting of all the geographic areas that could potentially contribute ancestor/immigrants to explain a given FAD (*i.e.*, because of their distance, environment, etc.). In practice, this will be a list of all of the adjacent biogeographic units. For each of these areas, one can score (1) whether there are rocks of the appropriate age (*i.e.*, same as or just younger than the FAD), environment, and preservational potential, (2) whether there are faunal studies from these rocks, (3) whether these studies include likely candidate ancestor/immigrants, and (4) whether potential immigrants could reasonably have moved from the source to the site of the FAD, via some reasonable reconstruction of paleogeography, currents, etc.

This technique has been applied to similar problems before. Allmon (1990) and Vermeij (2001), for example, assessed the completeness of global biogeographic surveys of groups of Cretaceous and Cenozoic gastropods by compiling large lists of fossil faunas of appropriate age for the groups in question. In applying this approach (which Allmon (1990) called the "faunal survey" method), one must keep in mind that such lists can be biased by the more detailed and thorough investigation of certain groups or areas as compared to others, as well as the inherent problems of high-resolution intercontinental correlation. Webster *et al.* (2003) suggested that unpublished data from museum collections can also aid in this purpose.

Test #2: Ghost ranges

"Ghost range" is the term for the gap between a taxon's actual evolutionary origination and its appearance in the stratigraphic record, which can be inferred in cases in which phylogeny and stratigraphy are not completely congruent and sister taxa appear to originate at different times (Norell 1992, Benton and Storrs 1994, Wills 2007) (Fig. 3). When the phylogeny of the group is known, ghost ranges can be calculated to find an implied origination time older than the FAD. These implied originations may indicate a significantly different pattern than raw FAD data, suggesting a test for the completeness or adequacy of the record; all other factors being

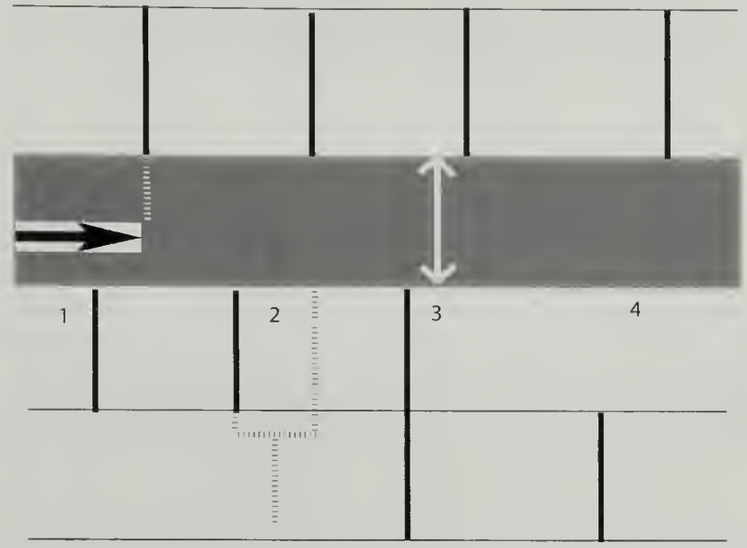

Figure 3. Four tests proposed here to evaluate the probability that a species' FAD (in stratigraphic unit 4) immediately above an unconformity approximates the time and place of that species' EFA. Test #1: Potential sources of immigration. What is the probability that the species immigrated rather than originated *in situ*? Test #2: Ghost ranges (dotted lines). What is the probability that the species originated before the hiatus marked by the unconformity? Test #3: Gap duration. What is the length of the hiatus? Test #4: Facies and sequence stratigraphy. Are the sedimentary environments below the unconformity likely to have been inhabited by the species? For example, the facies of unit 2 may never have contained the species, even though the species may have existed during this time, increasing our uncertainty that the species originated during the hiatus.

equal, shorter ghost ranges indicate a more complete stratigraphic record.

Test #3: Gap duration

Standard stratigraphic and geochronologic methods can be used to estimate the temporal duration of hiatuses at unconformities (*e.g.*, Allmon 1989, Paul 1998, Crampton *et al.* 2006b), and this can be compared to the observed duration of the taxon (Fig. 3). The ratio of the duration of the gap below a taxon's FAD (T) to the observed duration of the taxon (D) (which is of course also some function of its LAD) can be taken as a measure of the probability that a particular taxon actually originated at approximately the time and place of the FAD; lower ratios express higher probability.

Test #4: Facies and sequence stratigraphy

It is widely recognized that most marine fossil species tend to occur more commonly in some sedimentary facies than in others, and that much of this pattern reflects the ecological preferences of organisms (*e.g.*, Boucot 1981, Holland 2000). Many of the factors that control the geographic and environmental distribution of modern marine species are strongly correlated with water depth, which is also a major determinant of the structure of the stratigraphic record. That structure, as expressed in widely accepted stratigraphic models collectively known as "Sequence Stratigraphy" (Holland 2000, Coe *et al.* 2003), makes possible a set of predictions about the occurrence of fossils in outcrops (Holland 1995, 2000, Kidwell and Holland 2002) (Fig. 3). Under *constant* rates of origination and extinction, sequence stratigraphy predicts that:

Within a cycle of rise and fall in sea level, concentration of FADs (and LADs) is expected at the transgressive surface (TS, the point at which the shoreline migrates dramatically inland resulting in a rapid shift of depositional accommodation space shoreward, which in turn leads to lower sediment accumulation rates and even reworking on the shelf and formation of condensed beds offshore). The number of FADs at a TS should increase with both the degree of facies change across the surface and the temporal gap between the TS and the next oldest occurrence of the sedimentary facies immediately above the TS.

Concentrations of FADs (and LADs) are expected at sequence boundaries because of Unconformity Bias, and the number of FADs should increase with the length of the temporal hiatus at the sequence boundary.

Concentrations of FADs (and LADs) are expected in intervals of stratigraphic condensation (Holland 2000, Smith and Jeffery 2000). This Condensation Bias "alters perceptions of the relative timing of events, making events appear more closely spaced in time than they actually are" (Holland 2000: 157).

"Range offset", defined as the difference in age between the FAD of a species in a local stratigraphic section and its origination within the larger sedimentary basin, is expected to vary systematically within sequences, being large "within the transgressive systems tract of the deep basin [because of sediment starvation in the offshore as sea level rises], near the shelf break of the late highstand to early lowstand systems tract, and in extreme updip portions of shelves..." (Holland 2000: 157-158). ("Range offset" is equivalent to the difference between a species' FAD and its EFA if the EFA occurred in the same sedimentary basin.)

Based on these predictions, Holland (1995, 2000) suggested that the probability of finding each species in a stratigraphic section can be estimated by comparing its "preferred" facies to the distribution of that facies. In other words, the probability that a particular taxon actually occurred below its observed FAD can be estimated by whether that taxon would be expected to have occurred (and be preserved) in the sedimentary facies below that FAD. As illustrated in Fig. 3, if the facies immediately beneath an unconformity could reasonably be expected to have contained a species but does not, then we may have greater confidence that the observed FAD above that unconformity represents the approximate actual appearance of that species. If, on the other hand, the facies

immediately below the unconformity would not be expected to have contained or preserved the species had it existed at that time, then the actual evolutionary appearance of that species might have been significantly earlier.

Holland (1995, 2000) proposed a more detailed approach that could be applied either within or between facies, starting with making explicit estimates of three parameters for each species: peak abundance (PA), preferred depth (PD), and depth tolerance (DT), and then estimating paleo-depths through an outcrop. Our application here of the method to entire facies is justified because of the relative homogeneity within facies in the Coastal Plain Paleogene.

EXAMPLES FROM TURRITELLINE GASTROPODS

Turritelline gastropods (family Turritellidae, subfamily Turritellinae, *sensu* Marwick 1957a) are common components of many Early Cretaceous to Recent benthic marine assemblages worldwide (Allmon 1988, 2007), and frequently the most abundant macrofossils in assemblages in which they occur. They are taxonomically diverse, with more than 1800 described fossil and Recent species, appear to evolve relatively rapidly, and are among the most biostratigraphically important molluscan groups for their time interval; most species are (and probably were) largely sedentary suspension feeders, a mode of life unusual in caenogastropods (Allmon 1988, 2007). Here we use two recent but different analyses of species-level phylogenies in Late Cretaceous and Cenozoic turritellines from different parts of the world as case studies for application of the tests described above.

Paleogene of the U.S. Gulf and Atlantic Coastal Plains

A total of 55 turritelline species have been identified from Paleocene and Eocene sediments exposed on the Gulf and Atlantic Coastal Plains of the U.S. Allmon (1996) presented a phylogenetic analysis of 38 of these species (Fig. 4). Turritelline shells are morphologically relatively simple, with few discrete characters. This, together with the conclusion that the stratigraphic record of the Gulf and Atlantic Coastal Plain Paleocene and Eocene is relatively complete (Allmon 1989), justified the application of stratophenetic as well as purely cladistic techniques in phylogenetic analysis of turritellines from this interval (Allmon 1996).

The abundant, diverse, and well-preserved Paleogene mollusc faunas of the U.S. Gulf and Atlantic Coastal Plains have a long history of study (*e.g.*, Toulmin 1977). These faunas have long been known to exhibit a "stepped" or "punctuated" pattern of origination and extinction, in which blocks of relative faunal stability are interspersed with intervals in which as much as 90% of the fauna turns over, (*i.e.*, disappears and is replaced; Dockery 1984, 1986, Dockery and Lozouet 2003) even though the ecological changes at these transitions may not be nearly as profound (Sessa *et al.* 2010).

Test #1: Potential sources of immigration

Data available from Paleocene and Eocene mollusc faunas from the "total potential source area" of immigrants to the U.S. Gulf Coast (including West Africa (Adegoke 1977), Latin America (Allison and Adegoke 1969), California (Merriam 1941), and Europe (Cossmann 1912, Dockery 1984, Givens 1989)) suggest that some dispersal of marine gastropods, including turritellines, was indeed taking place during the Paleocene and Eocene (Allmon 1990). By comparing the taxa present in each of these potential source areas to Coastal Plain species at the time of their first appearance, it is possible to make a qualitative estimate of the probability that the Coastal Plain FADs represent immigration rather than true *in situ* origination. The results of this analysis (Allmon 1996) identified four instances (out of 38) in which immigration could plausibly be invoked (indicated by question marks in Fig. 4). Thus, all else being equal, this survey of potential sources of immigration suggests that most of these FADs probably represent in-situ origination.

Test #2: Ghost ranges

Because the phylogeny in Fig. 4 was not constructed using purely atemporal cladistics methods, recognition of ghost ranges in the strict sense of differences between a cladogram and observed stratigraphic ranges is not possible. Nevertheless, the phylogeny does permit some assessment of the completeness of inferred temporal durations of a number of species. For each species, we calculated a potentially "unpreserved" stratigraphic range as the duration between the observed FAD and the LAD of the most likely ancestor. The results indicate that 24 of 38 (63%) of the species have a potentially "unpreserved" range ("U") equal to or greater than their observed range ("O") (Table 3).

Test #3: Gap duration

The distribution of turritelline species in the Coastal Plain (Fig. 4) indicates that the majority (32 of 38, or 84%) of species show their first appearance immediately following hiatuses associated with cycles of sea level rise and fall. The duration of these hiatuses can be estimated and compared to observed species ranges. The results (Table 4) indicate that these gaps are all less than or equal to the mean observed species duration (3.6 million years, $\sigma = 0.5$).

Test #4: Facies and sequence stratigraphy

Following the approach of Holland (2000), we compared the occurrence of observed FADs of turritelline species at major unconformities in the Gulf Coastal Plain (Fig. 4) to the stratigraphic location of the next oldest sedimentary facies that might be expected to contain them (*i.e.*, based on their

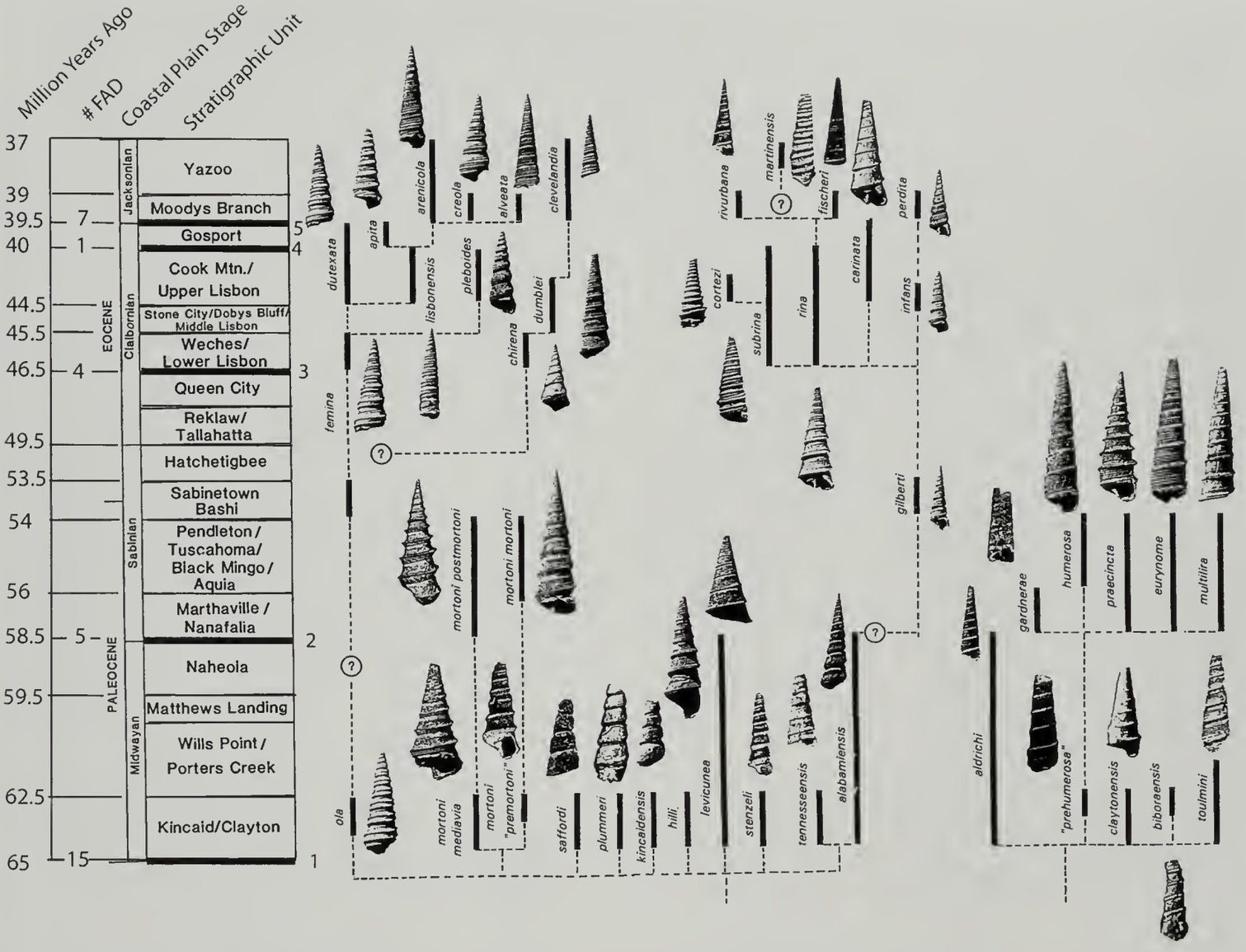

Figure 4. Phylogeny of turritelline gastropods from the Paleocene and Eocene of the U.S. Gulf and Atlantic Coastal Plains. Modified from Allmon (1996). Reproduced with permission.

observed pattern of facies occurrence). The results (Table 5) suggest that FADs at three of the five major unconformities occur in facies that lie directly on or very close to similar facies that lack the species (*i.e.*, have a high probability of representing the approximate EFA of their species). FADs at the other two major unconformities, in contrast, occur in facies that occur only well below the unconformity, and therefore have lower probability of approximating their respective EFAs.

Interpretation and application of results

Application of these four tests to the fossil record of Paleocene and Eocene turritelline gastropods of the U.S. Gulf and Atlantic Coastal Plains suggests that, although the overall stratigraphic record for this interval in this region is incomplete (Allmon 1989), a large proportion of the FADs of species in this clade appear to be relatively close to the EFAs, *i.e.*, are likely to be fairly reliable indicators of the approximate time and place of their actual evolutionary origination.

Although estimates of "unpreserved ranges" (analogous to ghost ranges) (Test #2, Table 3) suggests that more than half of the species have a potentially "unpreserved" range at least equal to their observed range, all of the estimated unpreserved ranges are less than half the length of the mean speciation interval for marine gastropods (14.9 million years) reported by Stanley (1979). The other three tests reflect even more favorably on the reliability of the record. The durations of the hiatuses associated with the five major unconformities are all less than or approximately equal to the mean observed species duration (3.6 million years) (Test #3, Table 4) (and

Table 3. Observed durations for the turritelline species shown (Fig. 4), compared to estimated unpreserved duration (see text for discussion). Observed durations modified from Allmon (1996), using numerical dates of stratigraphic units mostly from Baum and Vail (1988).

Species	Observed duration (my) (O)	"Unpreserved range" (my) (U)	Ratio U:O
alabamiensis	6.5	3.5 [4]	0.54
aldrichi	6.5	3.5	0.54
alveata	0.5	0.5	1.00
apita	0.5	0	0.00
arenicola	2.5	0.5	0.20
carinata	5.0	0	0.00
chireua	1.0	7.5	7.50
claytouensis	2.5	3.5	1.40
clevelaudia	2.5	4.5	1.80
cortezi	4.5	0	0.00
creola	0.5	0.5	1.00
duublei	1.5	0	0.00
dutexata	5.0	1.0	0.20
eurynome	4.5	4.5	1.00
femina	8.5	8.5	1.00
gardnerae	2.5	4.5	1.80
gilberti	0.5	4.5	9.00
hilli	2.5	3.5	1.40
humerosa	2.0	7.0	3.50
infans	1.0	0	0.00
kincaideusis	2.5	3.5	1.40
lisboueusis	4.5	1.0	0.22
levicuuea	6.5	3.5	0.54
mortoni mortoni [1]	10	4.5	0.45
uiortoni posmortoni [2]	11	3.5	0.32
multilira	4.5	4.5	1.00
ola	2.5	5.5	2.20
perdita	0.5	4.5	9.00
pleboides	4.5	1.0	0.22
plummeri	2.5	3.5	1.40
praecincta [3]	4.5	4.5	1.00
rina	6.5	7.0	1.08
rivurbana	0.5	0.5	1.00
saffordi	2.5	3.5	1.40
steuzeli	2.5	3.5	1.40
subrina	6.5	7.0	1.08
teuuesseensis	2.5	3.5	1.40
toulmini	2.5	3.5	1.40

[1] Allmon (1996) interpreted *Kapalmerella mortoni mortoni* as the direct anagenetic descendant of *K. mortoni premortoni*, thus the "observed" duration given here is the total from the FAD of *K. m. premortoni* to the LAD of *K. m. mortoni*.

[2] Allmon (1996) interpreted *Kapalmerella mortoni postmortoui* as the direct anagenetic descendant of *K. mortoni mediavia*, thus the "observed" duration given here is the total from the FAD of *K. m. premortoni* to the LAD of *K. m. mortoui*.

[3] Allmon (1996) recognized two subspecies of "*Turritella*" *praecincta*: "*T.*" *p. praecincta* from Alabama (with an observed duration of 4.5 my) and "*T.*" *p. virginiana* from Maryland and Virginia (with an observed duration of 2.0 my). The longer of the two is given here.

[4] The "unobserved" durations of all species in the Kincaid/Clayton is given as the estimated temporal gap across the Cretaceous-Tertiary boundary in the Gulf Coastal Plain (*i.e.*, between the Kincaid/Clayton and the Owl Creek/Prairie Bluff), 3.5 million years (Hazel *et al.* 1984).

again all are smaller than the mean speciation interval for marine gastropods). Similarly, analysis of the stratigraphic pattern of facies likely to contain fossils of these species above and below these unconformities (Test #4, Table 5) suggests that these patterns produce uncertainties greater than mean species durations at only two of the five major unconformities. Analysis of potential sources of immigration of these species (Test #1), furthermore, suggests that 90% of the first appearances have a high likelihood of being *in-situ* evolutionary events rather than immigration events.

This analysis does not mean that we can read the fossil record of these gastropods literally, and treat all first appearances as true evolutionary events. It does suggest, however, that these patterns of geological first appearances should not be wholly discounted as a source of evolutionary insight. Most (84%) of the species in Fig. 4 show their first appearances during hiatuses associated with five major unconformities. If we have reasonable confidence that this represents the actual time and place for most of these species, this suggests support for the "Common Cause" hypothesis (Peters and Foote 2002, Peters 2006). The association of first appearances of species with unconformities resulting from cycles of rising and falling sea level might, in other words, be telling us that transgressions and regressions of the shoreline (Fig. 2) could have played a significant role in the evolution of this group.

There is a long history of connecting faunal and sea-level changes in the Coastal Plain (*e.g.*, Palmer 1979, Baum and Vail 1988, Loutit *et al.* 1988). Dockery (1984, 1986), for example, argued that sea-level changes are primarily responsible for high faunal turnover in the Coastal Plain Paleogene, whereas Hansen (1987, 1992) argued for temperature changes (cooling) or extraterrestrial impact as the primary cause (Hansen 1987, Allmon and Ivany 2008, Sessa *et al.* 2010). Our results thus offer at least circumstantial support for sea-level as an important causal factor in speciation.

Table 4. Estimated duration of the five major unconformities shown in Fig. 4.

Unconformity	Duration (millions of years)	Notes
5	1.0?	(5)
4	0.6	(4)
3	<0.5?	(3)
2	1.0	(2)
1	3.5	(1)

(1) Cretaceous-Tertiary boundary: Hazel *et al.* (1984)

(2) Naheola-Nanafalia contact: Hazel *et al.* (1984)

(3) Tallahatta-Lisbon contact: Stenzel (1952) suggested that there was a significant hiatus between the Tallahatta and the Lower Lisbon in Alabama, but Hazel *et al.* (1984) disagreed. In Texas, the Tallahatta equivalent is a deltaic unit (the Queen City Formation) which interfingers with a fossiliferous marine unit (the Reklaw Formation). It is therefore possible that there was a minor hiatus at this time.

(4) Lisbon-Gosport contact: Hazel *et al.* (1984)

(5) Gosport-Moodys Brach contact: The contact between the Gosport and Moody's is clearly and sharply unconformable (*e.g.*, Dockery 1986), but a precise estimate of the length of the hiatus is difficult to obtain, in part because it was likely very brief. Both the Gosport Sand and the Moody's Branch Formation were placed in zone NP 17 by Siesser (1983) based on calcareous nannofossils. Zone NP17 has a duration of approx, 3.0 million years (*e.g.*, Staerker 1998). The time necessary for formation of these units is also unknown, but likely to have been brief; here we have used a figure of 0.5 my for each.

Cenozoic of New Zealand

The New Zealand Cenozoic mollusc record is one of the most abundant, diverse, and well studied in the world. The faunas have been extensively studied taxonomically (*e.g.*, Marwick 1929, Laws 1934a, 1934b, 1940, Fleming 1955, Beu 1970, Maxwell 1978, 1992, Beu and Maxwell 1990, Stillwell 1993, Beu 2004, 2006), and used for paleoenvironmental reconstruction (*e.g.*, Fleming 1944, Beu 1974), biostratigraphy (*e.g.*, Beu 1969, Cooper *et al.* 2001, Cooper 2004), and examinations of diversity patterns (*e.g.*, Beu 1990, Crampton *et al.* 2003, 2006a, Hendy 2007, Hendy *et al.* 2009).

Turritellines are an important component of the New Zealand Cenozoic mollusc record (*e.g.*, Marwick 1957a, 1957b, 1971, Beu 2010), with nine genera occurring through the Cenozoic. Three of these genera (*Zeacolpus* [Finlay, 1926], *Stiracolpus* [Finlay, 1926], and *Maoricolpus* [Finlay, 1926]) also have species still extant around the coast of New Zealand. As with turritellines of other geographic regions (Allmon 2007), New Zealand fossil and Recent turritellines are often found in high abundances (*e.g.*, Grace and Hayward 1980, Hayward *et al.* 1981), and are ecologically important components of the faunas in which they are found.

Three peaks of FADs have been observed in the total New Zealand Cenozoic molluscan fauna (Beu 1990, Beu and Maxwell 1990): the Middle Eocene, Middle Oligocene, and Early Pliocene. These FAD peaks are not highly correlated with standing diversity of the molluscan fauna (Beu 1990, Crampton *et al.* 2006a, Hendy 2007), which peaked in the Middle Miocene, but there are increases in diversity at these times when compared to the stages immediately before and after.

The Cenozoic turritelline fauna of New Zealand includes approx. 60 species (Beu 2010, Smith 2011). The FADs of these species show a generally constant low level through the Cenozoic, from the first appearance of the subfamily in the Paleocene. The two most species-rich New Zealand

Table 5. Sequence stratigraphic analysis of completeness of the fossil record of turritelline gastropods in the Paleocene and Eocene of the U.S. Gulf Coastal Plain (based on the phylogeny and species ranges shown in Fig. 4).

Unconformity	Overlying stratigraphic unit containing FAD	Number of species FADs	Next oldest similar facies	Mean temporal gap (my) between FAD and next oldest similar facies
5	Moodys Branch	7	Gosport [1]	≅ 0
4	Gosport	1	Upper Lisbon/ Cook Mtn. [2]	≅ 0
3	Weches/Lower Lisbon	4	Reklaw/ Bashi [3]	3.0-7.0
2	Nanafalia	5	Naheola/ Matthews Landing [4]	< 1.0
1	Kincaid/Clayton	15	Owl Creek/ Prairie Bluff [5]	4.0

[1] Both the Gosport and Moody's Branch are glauconitic, high-density shell beds (Toulmin 1977, Baum and Vail 1988).

[2] Although they are not glauconitic, high-density shell beds like the Gosport, the Lisbon and Cook Mountain formations are highly fossiliferous and contain a high species diversity of molluscs, including many in common with the Gosport (Toulmin 1977, Dockery 1980), suggesting similar preservation potential.

[3] The Reklaw Formation of Texas contains a low density of fossils, but a very high diversity of species represented by very well-preserved specimens (Garvie 1996). The correlative Tallahatta Formation of Alabama and Mississippi, however, has only rare and very poorly-preserved fossil molluscs. The next oldest comparable facies to the Lower Lisbon in the eastern Gulf region if the Bashi Formation.

[4] Although the Naheola Formation of Alabama does contain fossils of some species in common with the overlying Nanafalia, not all are well-preserved, suggesting some difference in preservation potential. The Matthews Landing beds, however, have an extremely well-preserved and very diverse molluscs fauna.

[5] The Owl Creek and Prairie Bluff formations of Tennessee, Mississippi, and Alabama contain occasional shell beds with diverse, abundant, and well-preserved molluscs (Sohl 1960, Mancini *et al.* 1995).

turritelline genera are *Zeacolpus* (23 species) and *Stiracolpus* (30 species), whose FADs show a pattern approximately the same as the group as a whole, from the appearance of *Zeacolpus* in the Middle Eocene, with smaller peaks of FADs in the Miocene (*Zeacolpus*) and Pliocene (*Stiracolpus*) (Fig. 5). A recent phylogenetic analysis of *Stiracolpus* and *Zeacolpus* (Smith 2011) (Fig. 6) makes possible a more detailed analysis of this record.

Test #1: Potential sources of immigration

Peaks of FADs in both *Zeacolpus* and *Stiracolpus* occur in the first stages in which they both occur—the Bortonian (Middle Eocene) for *Zeacolpus* and Opoitian (earliest Pliocene) for *Stiracolpus* (Fig. 5). This is also where there are peaks in EFAs based on ghost ranges (see below) that occur in both genera (though part of this pattern may be an artifact due to the age of the outgroup used in calculating the phylogeny [Smith 2011]). Both of these stages also show peaks of first appearances in the rest of the molluscan fauna (Beu and Maxwell 1990), and intervals in which calculated origination rate (see below) is high (Crampton *et al.* 2006a). The first of these, the Middle Eocene Bortonian peak in total molluscan FADs, has previously been explained as due to immigration of much of the fauna, including *Zeacolpus*, into New Zealand at that time (Beu and Maxwell 1990), though the source of the immigrants is not clear. Part of the high rates of total molluscan FADs in the Middle Eocene Bortonian stage may also be due to the relatively long duration of that stage (Crampton *et al.* 2006b).

The peak in FADs in *Stiracolpus* at the base of the Pliocene corresponds with the appearance of a previously recognized

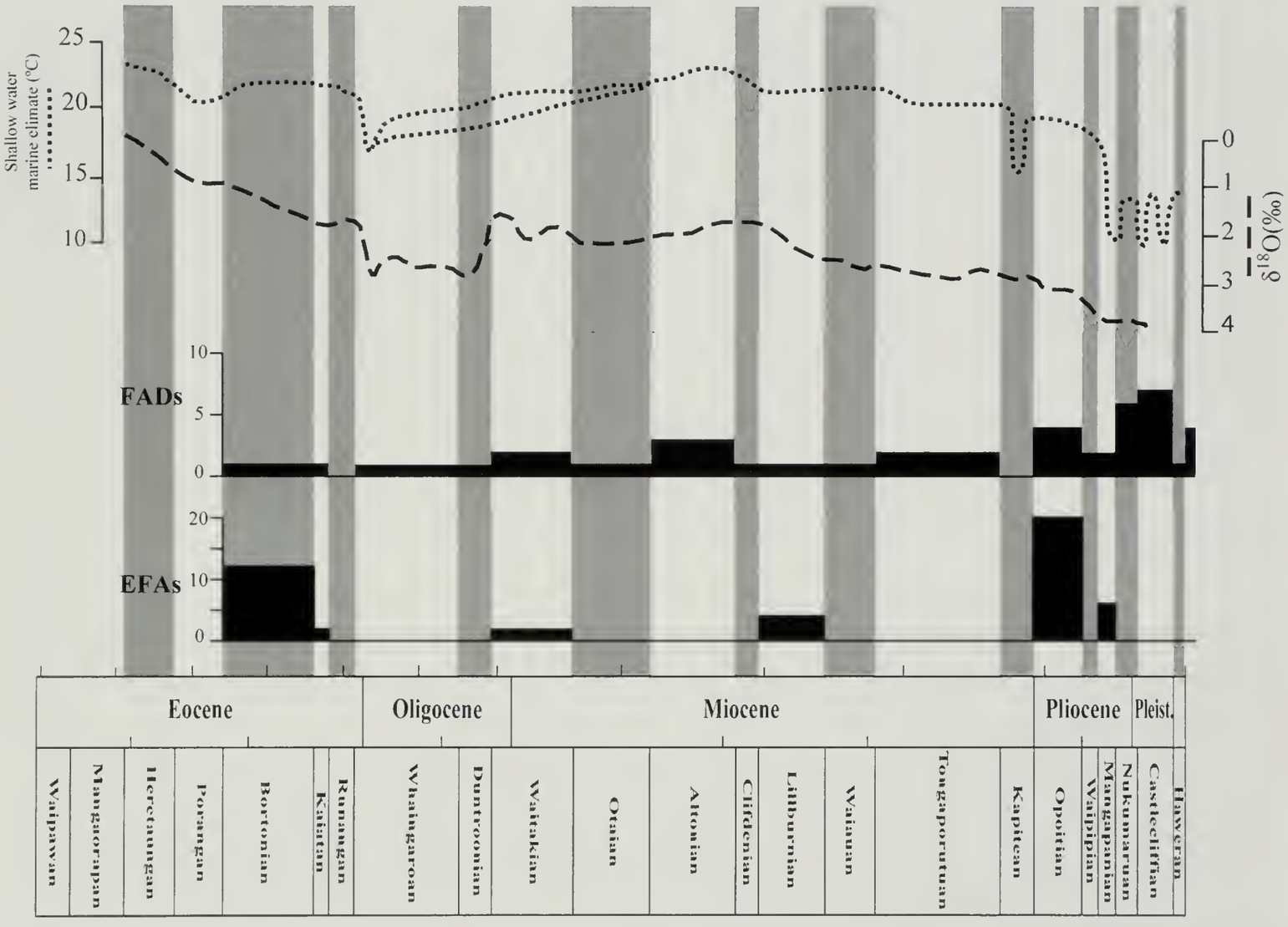

Figure 5. Number of FADs of *Stiracolpus* and *Zeacolpus* species per stage in the New Zealand Cenozoic from the first appearance of *Zeacolpus* in the middle Eocene to Recent, and number of calculated originations (EFAs) per stage for *Stiracolpus* and *Zeacolpus* based on ghost ranges implied by a phylogenetic analysis of each genus (Fig. 6). Shallow water marine temperature (dotted line) adapted from Hornibrook (1992), $\delta^{18}O‰$ curve (dashed line) adapted from Zachos *et al.* (2001).

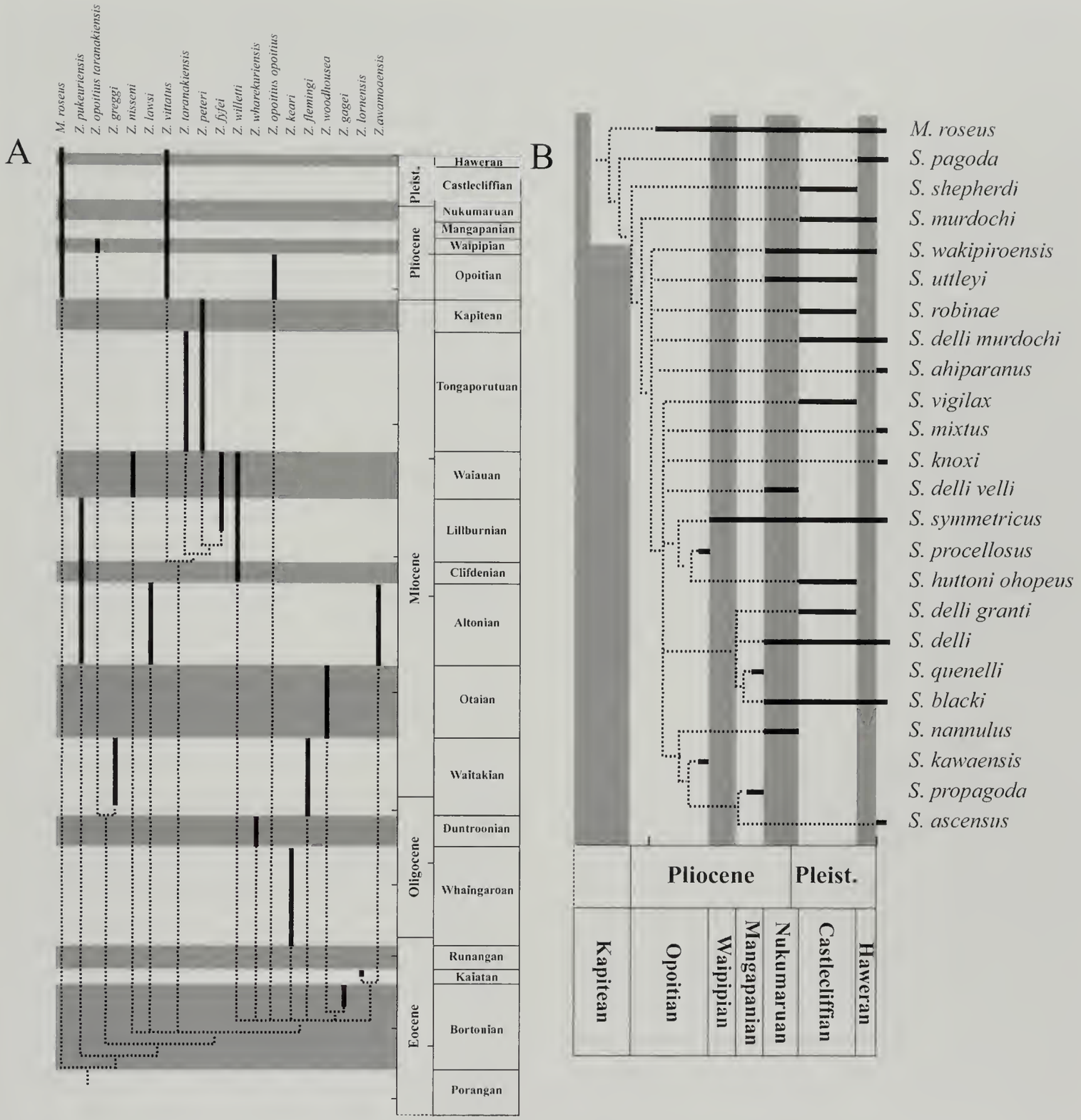

Figure 6. Phylogenies of *Zeacolpus* (A) and *Stiracolpus* (B) from Smith (2011), plotted on the New Zealand time scale's stages (Cooper 2004). Both phylogenies are frequency difference consensus trees from phylogenies generated under a number of different weighting schemes using both traditional characters (from protoconch and teleoconch) and characters from a geometric morphometric analysis. Solid black lines indicate the stages from which a species has been reported but do not necessarily imply that species is present through the entire stage. Dotted lines indicate implied ghost range inferred from phylogeny. Species ranges have occasionally been shortened to not range through an entire stage in order to accommodate branching events inferred to occur within that stage. Such "shortened" ranges do not imply that species occurred only in the later part of that stage.

cooler-water fauna that began to appear in New Zealand at the end of the Miocene, presumably due to intensification of the circum-Antarctic current (Fleming 1965, Beu 1990, Beu *et al.* 1997) and in conjunction with a major ecological turnover (Hendy *et al.* 2009). The majority of *Stiracolpus* species from this interval are geographically restricted, and it is therefore possible that some species could have immigrated from other basins elsewhere in New Zealand. For instance, Beu (2004) shows that there are occurrences of warm-water species within the Wanganui Basin (where the majority of *Stiracolpus* species are found) in the south-west of the North Island, which probably originated in the north-east of the North Island and were intermittently transported as larvae through temporary seaways.

Although immigration is a likely explanation of the generic first appearance of both *Zeacolpus* and *Stiracolpus* in New Zealand, it seems less likely that multiple species of each genus immigrated at the same time; in the case of *Zeacolpus* the phylogeny in Fig. 6 suggests at a minimum 10 species, and in that of *Stiracolpus*, 12 species. Speciation *in situ* following immigration seems a more likely explanation simply from a probabilistic point of view. Immigration into New Zealand has evidently occurred in other genera of turritellines at other times, *e.g.*, *Maoricolpus* appears to have originated in Australia and transferred to New Zealand, later becoming extinct in Australia while in New Zealand it survived until the Recent (*e.g.*, Allmon *et al.* 1994).

Test #2: Ghost ranges

Cladistic phylogenies of the two genera *Zeacolpus* and *Stiracolpus* (Smith 2011) imply ghost ranges for every included species of both genera (Fig. 6). The originations implied by these phylogenies show a very different pattern than the raw FADs for both genera (Fig. 7), with originations occurring in bursts, rather than gradually through time, and with considerable ghost ranges being implied for nearly every species. (These bursts of inferred EFAs are partially due to the choice of outgroup in the phylogeny—a different outgroup with an older stratigraphic range may have elongated the ghost ranges even further [Smith 2011] but there is only one New Zealand turritellid species that occurs before the oldest *Zeacolpus* species in the analysis, and therefore this conservative selection of outgroup seems justified.) U:O ratios (Table 6) indicate unpreserved ranges greater than the observed ranges in nearly all cases. In *Zeacolpus* the mean U:O value is 6.32 while in *Stiracolpus* it is 80.47 (although if species only observed in the Recent are excluded, this drops dramatically to 2.37). It is important to note that the observed ranges used to calculate these ratios are taken as spanning the full length of any stage in which the species is found, making O in all cases likely larger than was actually the case. These ratios are thus actually conservative estimates.

The ghost ranges calculated are long, but not exceptionally so for marine invertebrates (*e.g.*, Wills 2007 and references therein). The maximum range extension implied is approx. 35 million years in *Zeacolpus*, but in the pre-Pliocene record of New Zealand, such range extensions are not implausible, as fossil occurrences are usually highly localized. In *Stiracolpus*, the ghost ranges implied by the phylogeny are up to ~6 million years for a species known only from the Recent. Although such ranges may not be unusual for most groups, it is almost the entirety of the total stratigraphic range of the species in New Zealand, implying that there is an extensive gap in the fossil record of this genus. Given the resolution and highly fossiliferous nature of the majority of the beds of the New Zealand Pliocene and Pleistocene basins, ghost ranges extending through the majority of the Plio-Pleistocene would appear to be unlikely. Immigration from other basins (*e.g.*, Beu 2004) could account for some of the ghost ranges but their extent and ubiquity suggests immigration cannot explain them all.

Test #3: Gap duration

In order to assess gap duration it is necessary to know not just the duration of the species and the duration of the hiatus during which it may have originated, but also to what degree a hiatus may be directly associated with a particular FAD (*i.e.*, does the FAD occur immediately above the hiatus, or somewhere within the overlying facies). This requires a level of stratigraphic resolution sufficient to determine the duration between an FAD and an underlying unconformity. This level of resolution, however, is unfortunately not available for the majority of *Zeacolpus* species, and so we cannot directly associate hiatuses with FADs or calculate hiatus length. Another approach to analysis of *Stiracolpus*, however, may be more profitable.

Stiracolpus occurs in the Pliocene and Pleistocene, the stratigraphic record of which in New Zealand is much better resolved than the earlier stage of the Cenozoic. This portion of the stratigraphic record is one of the most complete in the world (*e.g.*, Naish *et al.* 1998, Saul *et al.* 1999) with very little time being unrepresented, mostly hiatuses within cyclothems in the stratigraphic sequences. Values for T can therefore be much better constrained in this stage than earlier, as it consists of well-dated and well-constrained cyclothems corresponding to the 41,000 and 100,000 year Milankovitch cycles (Abbott 1998, Carter and Naish 1998). A conservative estimate of hiatus length within one of these cyclothems might be 10,000 years, which is almost certainly an overestimate given the completeness of the sequences and lack of missing material and time in the cyclothem sequences (Abbott 1998). Using this estimate, however, we can calculate observed durations (D) for species of *Stiracolpus*. (There are multiple other sources of error in this calculation; for instance, D will be an

Table 6. Observed durations for the New Zealand fossil species in the genera *Stiracolpus* and *Zeacolpus* shown (Fig. 6), compared to estimated unpreserved duration. Data from Smith (2011).

Species	Observed duration (my) (O)	"Unpreserved range" (my) (U)	Ratio U:O
S. ahiparanus	0.01	4.51	451.00
S. ascensus	0.01	3.00	300.00
S. blacki	2.41	0.77	0.32
S. delli	2.41	0.60	0.25
S. delli grauti	1.29	1.37	1.06
S. delli murdochi	1.64	2.88	1.76
S. delli velli	0.77	2.88	3.74
S. huttoni ohopeus	1.29	3.65	2.83
S. kawaensis	1.68	0.00	0.00
S. knoxi	0.01	5.28	528.00
S. mixtus	0.01	5.28	528.00
S. murdochi	1.63	3.65	2.24
S. nannulus	0.77	2.88	3.74
S. pagoda	0.35	6.16	17.60
S. procellosus	1.68	0.00	0.00
S. propagoda	0.60	0.00	0.00
S. quenelli	0.60	0.00	0.00
S. robinae	1.29	2.88	2.23
S. shepherdi	1.29	3.65	2.83
S. symmetricus	3.61	1.68	0.47
S. uttleyi	2.06	2.88	1.40
S. vigilax	1.29	2.88	2.23
S. waikipiroensis	2.40	2.88	1.20
Z. awamoaensis	3.10	18.00	5.81
Z. flemingi	3.50	17.80	5.09
Z. fyfei	4.18	0.00	0.00
Z. gagei	6.00	0.00	0.00
Z. greggi	3.50	0.00	0.00
Z. keari	7.00	8.70	1.24
Z. lawsi	3.10	27.10	8.74
Z. lorneusis	1.00	0.00	0.00
Z. nisseni	1.78	30.30	17.02
Z. opoitius opoitius	1.68	40.62	24.18
Z. opoitius taranakiensis	1.68	39.40	23.45
Z. peteri	5.64	4.18	0.74
Z. pukeuriensis	6.30	24.00	3.81
Z. taranakiensis	4.42	4.18	0.95
Z. vittatus	5.28	9.82	1.86
Z. wharekuriensis	2.10	15.70	7.48
Z. willetti	4.98	27.10	5.44
Z. woodhousea	2.70	21.30	7.89

[1] Species observed only in the Recent are assumed to have an observed range (O) of 10,000 years.

[2] *Stiracolpus murdochi* used here is an unpublished species described by Marwick in the GNS collections.

overestimate as total species duration is calculated by summing the total length of any stage in which that species occurs.) Calculated this way, the average D of *Stiracolpus* species is 1.27 million years—orders of magnitude greater than a 10,000 year hiatus. These figures could be better constrained in the future given the level of stratigraphic resolution available in the Plio-Pleistocene basins of New Zealand.

A more precise estimate can be made for the seven species of *Stiracolpus* that have FADs in the Castlecliffian stage (approximately equivalent to the start of the Pleistocene—the Plio-Pleistocene boundary actually falls towards the end of the previous stage, the Nukumuruan [Cooper 2004]). At the unconformity between the Nukumuruan and the Castlecliffian stages there is a 500,000 year hiatus (Abbott *et al.* 2005). Of the seven species of *Stiracolpus* having FADs at in the Castlecliffian stage, five are known only from the Castlecliffian (stage length = 1.29 million years), one of which extends into the Haweran (stage length = 0.34 million years) and one of which is present in the Recent. The average duration (D) of these species is 1.76 million years, which is approximately 3.5 times longer than the length of the hiatus (T) of 0.5 million years.

Test #4: Facies and sequence stratigraphy

The patchy geographic distribution and low temporal resolution of much of the pre-Pliocene strata of the New Zealand Cenozoic make a sequence stratigraphic approach difficult, as it requires correlation of co-temporal stratigraphic events at a higher resolution than currently possible. New Zealand has been tectonically active during most of the Cenozoic, and calculating local sea level variation is thus very difficult. There is therefore not a well-constrained sea level curve available for the majority of the New Zealand Cenozoic (Crampton *et al.* 2006a). However, five second-order sequence stratigraphic cycles—*i.e.*, cycles influenced only by tectonics rather than eustasy—have been identified from the Eocene to the Recent (King *et al.* 1999, Crampton *et al.* 2006b). Although a widespread transgression in the Bortonian has been identified (Beu and Maxwell 1990), which could be associated with an apparent peak in

speciation in *Zeacolpus* during this stage, it is harder to identify sea level variations that correspond to the other peaks in FADs or calculated origination in either genus. In cases in which other peaks do correspond with some variation in sea level, it is not necessarily a drop (for instance, the peak in the Waitakian [Early Oligocene] actually corresponds with the period of maximum flooding of New Zealand [Wilson 1956, Crampton *et al.* 2006b: fig. 6] during a first order sequence stratigraphic cycle rather than a drop in sea level).

Crampton *et al.* (2006b) have shown that sampling probability in the New Zealand Cenozoic molluscan shelf fauna is linked to the second order sequence stratigraphic cycles, with highest sampling probability occurring during mid-cycle, due to enhanced preservation potential during these periods in addition to erosional loss at sequence boundaries. These peaks in sampling probability coincide with peaks in FADs in *Zeacolpus* and *Stiracolpus* (but only the two in the Middle Eocene and Lower Pliocene also correspond with peaks in calculated originations). The high number of FADs in these stages may be at least partially a sampling artifact due to low sampling intensity in prior stages. The Late Miocene (immediately prior to the first appearance of *Stiracolpus*) contains a high proportion of bathyal rather than shelf facies in which molluscs are less frequent, whereas the Paleocene to Early Eocene (prior to the appearance of *Zeacolpus*) is poorly represented in the New Zealand rock record. Other genera of turritellines have their FADs in the same stage as *Zeacolpus* (*e.g.*, *Amplicolpus*) but the previous turritelline occurrence prior to this stage occurred in the Lower Paleocene, approx. 20-25 my previously. It is, therefore, theoretically possible that the EFA of *Zeacolpus* could be up to 25 My before the first *Zeacolpus* FAD.

As mentioned above, however, the Pliocene and Pleistocene basins of New Zealand consist of stacked series of cyclic shallow-marine strata (*e.g.*, Naish *et al.* 1998, Saul *et al.* 1999). These sequences are well exposed on land (due to uplift along the boundary of the Pacific and Australian plates (Naish 2005), and have been intensively studied since Fleming (1953) first described the fossiliferous sections of the Wanganui Basin (*e.g.*, Vella 1963, Beu and Edwards 1984, Kamp and Turner 1990, Abbott and Carter 1994, 1999, Pillans *et al.* 1994, Naish *et al.* 1998, 2005a, 2005b, Saul *et al.* 1999, Abbott *et al.* 2005, Turner *et al.* 2005). Although detailed bed-level analyses have not yet been carried out on the New Zealand turritellines to compare FADs and ghost ranges horizon-by-horizon through the Plio-Pleistocene, this is an area where the techniques used here could be profitably employed.

Interpretation and application of results

The records of turritellines in the Paleogene of the U.S. Coastal Plain and the New Zealand Cenozoic show important differences, both in the temporal resolution of the record and (to the degree that conclusions are possible) in apparent evolutionary responses to environmental variation. Although peaks of FADs for *Zeacolpus* do correspond with periods of high sampling probability (*sensu* Crampton *et al.* 2006a, 2006b), taken as a whole the pre-Pliocene fossil record of turritellines in New Zealand appears to be of only limited utility for drawing useful conclusions about the evolutionary significance of observed FADs. The Plio-Pleistocene record, however, appears to show more potential.

Test 1 suggests that *Zeacolpus* immigrated into New Zealand from elsewhere, and then probably speciated *in situ* afterwards. The under-sampling of the stages immediately prior to the appearance of each genus means that this speciation may not have occurred within a single stage, but could have happened over a longer time period. This is particularly true in the case of *Zeacolpus*, where there are multiple poorly represented stages prior to the first appearance of the genus in the Bortonian. The very long ghost ranges of test 2 also suggest that the stratigraphic record is very incomplete. Many of these ghost ranges pass through stages that have a high sampling probability (Crampton *et al.* 2006a), in which it would be expected that fossils would be found if the species was present. The geographic patchiness of the pre-Miocene record, however, could mean that exposure is not available in the areas in which the species might be expected even if the correct time period is sampled.

This is less likely to be the case in the Pliocene and Pleistocene. Although tests 1 and 2 suggest that FADs of *Zeacolpus* and *Stiracolpus* may not be accurate representations of when species actually originated, test 3 is more hopeful at least in the case of *Stiracolpus* where hiatuses in the stratigraphy of the basins are very short compared to the duration of species. The hiatus at the base of the Castlecliffian stage of 500,000 years, while longer than others in these sequences, is still short compared to species duration and is of a magnitude in which speciation is observed in other species. While hiatuses underlying FADs in *Zeacolpus* may also be of similar magnitude, it has not been possible to test this here.

EFAs and, to a lesser extent, FADs in the two turritelline genera here appear to show some correlation with cool periods (Fig. 5). Though some of the peaks in both FADs and EFAs may be artifactual (*e.g.*, due to poor sampling in previous stages), this cooling pattern appears to be the only consistently identifiable factor associated with periods of high origination in these two genera. Decreases in temperature have normally been associated with extinction events rather than speciation (*e.g.*, Hansen 1987, 1988), but decreasing temperature could also lead to allopatic speciation through vicariance (*e.g.*, Evans *et al.* 2005) in a similar way as sea level fall (Fig. 2). In the case of either temperature or sea level change being correlated with inferred speciation in *Stiracolpus*,

it is interesting to note that despite the glacial cycles throughout the majority of *Stiracolpus*'s range of six stages and the Recent, apparent originations only occur in two of these. This suggests that the factors causing speciation are more complex than just sea level or temperature variation. Sea level variation thus might be less important in the evolution of New Zealand turritellines than for Gulf Coast species though it may be in some way correlated due to association between environmental variables. For instance, sea level change is often associated with periods of cooling, due to the formation of glaciers as in the Pliocene and Pleistocene, while other sea level changes during the New Zealand Cenozoic may be coincident with temperature variations (*e.g.*, Beu and Maxwell 1990).

Better resolved temperature and sea level curves are beginning to be produced for the Pliocene and Pleistocene of New Zealand than are available for the pre-Pliocene (*e.g.*, Carter 2005) and these, in conjunction with modern sequence stratigraphic models of these basins, should allow more detailed analyses of speciation events in *Stiracolpus*, and specifically allow tests 3 and 4 to be applied with greater accuracy. Future detailed correlation of formation-level origination data with the sequence stratigraphy and oxygen isotope stages may help to clarify why speciation does not appear to occur in *Stiracolpus* after the end of the Pliocene when examining ghost ranges while raw FAD counts indicate more gradual appearances.

DISCUSSION/CONCLUSIONS

What then can we reasonably expect the fossil record to contribute to our understanding of speciation in marine gastropods? The first answer is a failing of neontology rather than paleontology: data from modern marine gastropods are not yet adequate to provide a clear set of expectations that we can readily apply to the fossil record. The information that is available (on both cryptic species and phenotypic variation) seems to indicate that, although morphospecies based on shell form can frequently be roughly equivalent to reproductively isolated evolutionary units, caution should be used when recognizing species of marine gastropods in the fossil record. Similarly, although there is abundant evidence for allopatric speciation in modern marine gastropods, suggesting that patterns consistent with such processes can usefully be sought in the fossil record, there is also abundant evidence for non-allopatric speciation. More study is needed to determine the relative frequency of these different modes among modern forms, and whether or how non-allopatric processes might be recognizable in fossils.

If we make the assumption that allopatry is the most frequent mode of speciation in marine gastropods, the few studies that are available hint at some general patterns. For example, some recent studies of geographic range of fossil gastropods at the faunal level suggest that taxa with narrower ranges have higher rates of speciation, perhaps because those attributes that contribute to wide geographic range also suppress allopatric speciation (*e.g.*, Jablonski and Roy 2002). Many more such studies are needed to test the generality of this result. Several studies of individual clades also show a negative relationship between geographic range and origination rate (*e.g.*, Hansen 1978, 1980, Allmon 1996). Together with studies of modern species, these results suggest at least one potential solution to the "paradox of marine speciation". At least in gastropods, a combination of temporal environmental change and environmental heterogeneity can create numerous opportunities for small-scale allopatry. Environmental changes may fragment large geographic ranges and reduce local population sizes. Under these conditions, environmental heterogeneity that might be less significant within larger geographic ranges can produce and maintain barriers for sufficient time to allow genetic differentiation.

Among both paleontologists and neontologists, the assessment and use of the fossil record as a source of insight about speciation are contradictory; it is sometimes hailed as a unique source of the perspective of "deep time" and at other times assailed as so incomplete as to be essentially useless. Yet, as other authors have noted (*e.g.*, Kidwell and Flessa 1996, Behrensmeyer *et al.* 2000, Kidwell and Holland 2002, Paul 2009), the fossil record is neither entirely trustworthy nor entirely misleading. Rather, we must learn to assess the character of its data on a case-by-case basis, depending on the questions that we are asking.

Despite the substantial analytical attention that has been given to the nature and completeness of paleontological data, we are just beginning to develop and use the tools that are necessary to evaluate the record as a serious source of data about the origin of species. The tests we present here do not provide comprehensive assessments of the adequacy of any particular fossil record to inform us about speciation, but the results we have discussed here suggest that, if a single record is examined from many angles and using many kinds of information, a more comprehensive assessment of its adequacy for addressing particular evolutionary questions can be developed. The results we report here are only semi-quantitative. They can compare one record with another, to evaluate which is more reliable, but they cannot estimate with great precision the actual length of time between the EFA and FAD of a particular species, nor assess statistical significance of the patterns they reveal. These necessary aspects await further work.

The two particular fossil records of Cenozoic turritelline gastropods examined here demonstrate both the challenges and some of the opportunities inherent in the shallow-shelf marine fossil record. It is not so much the "incompleteness" of the record that limits our ability to test hypotheses and

draw conclusions, but its temporal resolution. At least one of the examples considered here is consistent with the emerging neontological hypothesis that small-scale allopatry, caused by environmental change and heterogeneity, is at least occasionally an important process in the evolution of some caenogastropod clades inhabiting shallow marine shelves. Future paleontological analyses—which take the completeness of the record adequately into account—could build on these results and begin to compile a database of relative frequencies of such environmental-evolutionary linkages in the context of explicit models of evolution, rather than just large-scale correlation. To the degree that this occurs, the fossil record could eventually become a source of significant insight about the processes of speciation.

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